

The University of Chicago

SEEDLING ANATOMY OF CANNABIS
SATIVA L.

A DISSERTATION SUBMITTED TO THE
FACULTY OF THE DIVISION OF THE
BIOLOGICAL SCIENCES IN CANDIDACY
FOR THE DEGREE OF DOCTOR OF
PHILOSOPHY

DEPARTMENT OF BOTANY
1936

By
ANTON HELMER BERKMAN

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Introduction

The true hemp plant, Cannabis sativa L., a member of the Moraceae, is one of major economic importance. Several forms of the plant have been described under different names, but in general botanists regard the genus as monotypic and recognize only the one species. The place of its origin as well as the history of its specific name appear to be rather obscure. De Candole (4) after studying the geographical distribution of uncultivated varieties of the plant, suggested a region east of the Caucasus as its home, but arrived at no definite conclusion. Dewey (5), on the other hand, who made a critical investigation of hemp culture, after a careful survey of ancient Asiatic historical evidence, concluded that hemp was probably the earliest plant cultivated for a textile fiber and that Central Asia was the original home of the species.

According to Dewey (5), the name Cannabis sativa is of unknown derivation and the first application of its use to the hemp plant occurs in Dioscorides' *Medica Materia* of 1547 A.D. Cultivation of the species has resulted in the development of three distinct types or groups of forms, with few recognized varieties in any one group. Two types with their varieties are grown in Europe and Central Asia, one specifically for the raw fiber product and the other for the fruit which is utilized as a source of oil and as a food. In the Americas different varieties of the fiber type are cultivated, but on a smaller scale than in Europe and Asia where the United States of Soviet Russia leads in production and exportation of the raw fiber material. The third group is cultivated in India, Arabia, and Northern Africa as a source of the narcotic drug called "bhang," "ganja," "hasheesh," and "charas," etc., in the Orient, and marihuana in the western hemisphere.

With the exception of the studies of Van Tieghem and Douliot, and Flahault on root development most of the investigations on hemp have centered on the anatomy of the mature stem

(Breedemann, 1; Briosi and Tognini, 2; Herzog, 8; Matthews, 12; Saito, 16), the flower and fruit (Muth, 13; Prain, 15; Winton, 20). The present paper deals primarily with an account of the seedling development.

Methods and Materials

Feramington and Kentucky commercial varieties of hemp were used in this investigation. Both were grown in the greenhouse at the University of Chicago during the winter and spring and compared with material of these varieties which were grown outdoors during the spring and summer months at El Paso, Texas. Seedlings from these sources exhibited no morphological differences, except that the hypocotyls of those grown in the greenhouse elongated more rapidly. Both fresh and stained material was studied. Of the several killing agents and stains tried, a modification of Nawaschin's solution (Crooks, 3) and Flemming's triple stain, respectively, were found most satisfactory. The material prepared consisted of mature embryos, seedlings 18-24 hours old, and roots, hypocotyls, and cotyledons 3-15 days old. The 3-5 day old material proved best for studies of the primary tissues. The serial sections mounted were 5-12 microns in thickness.

Drawings, with the exception of Plates I and II and Figure D of Plate V, were prepared by using a technique employed by McCall (11), except that a potassium iodide-iodine solution and a hyposulphite of soda solution as described by Naylor (14) were substituted for potassium cyanide-iodine solution. Briefly stated, this process consists of four principal steps. First, a 5-by-7-inch photomicrograph is made of the desired section; second, an enlargement about two hundred times that of the original section is obtained; third, the enlargement is inked with water proof India ink, checking the lines with the original object; and fourth, the photography is bleached out with a solution of potassium iodide-iodine and the iodine color is removed with a solution of hyposulphite of soda. The result after washing and drying is a black and white line drawing. Care is necessary in handling the drawings while they are wet because the ink lines smear readily when the paper is moist.

The Fruit, Seed, and Embryo

The fruit of the hemp plant is a light brown to dark gray or mottled achene, orbicular or oval in form. Its size and color may vary within the particular variety. Lubbock (10) gives 1.5-2 mm. as the diameter of the fruit, while Dewey (5) describes it as 2.5-4 mm. in thickness and 3-6 mm. long. Numerous measurements made on fruits of both varieties used in this study agree with Dewey's figures. The membranous seed coat is invaginated between the cotyledons and the radicle and is marked by three distinctly colored zones. The portions which cover the cotyledons and the radicle are sage-green and olive-green in color, respectively, while that round the chalaza is brown. The endosperm lies immediately within the seed coat and surrounds the entire embryo. It is not uniform in depth as the lenticular portion which lies between the cotyledons and the radicle is 7-10 cell layers in thickness while the remainder covering the embryo varies from one to five layers.

The embryo which is curved so that its axis assumes a u-shape consists of two plano-convex cotyledons which enclose between them a well developed epicotyl and a sub-cylindrical radicle. The orientation of the axis is such that the tip of the radicle and the apices of the cotyledons point to the chalazal end of the seed which is directed towards the stylar end of the ovary (Plate II, Fig. A).

Germination of the Seedling

Van Tieghem (19) gives 31.5 C. and 42.5 C as the optimum and maximum temperatures respectively for hemp seed germination. No minimum is reported. In the present investigation, fruits were planted at temperatures ranging from 15.5-37.7 C. At 29.5-35 C. the hypocotyls appeared above ground within 48 hours, while at lower temperatures the seedlings failed to come above ground before 60-72 hours had elapsed. In each range of temperature the radicle emerged from or at least broke open the fruit coat, indicating that the delay at the lower temperatures was probably due primarily to failure of the hypocotyl to elongate rapidly.

In the process of germination, the radicle emerges from the fruit coat through the styler end, splitting the coat into two halves which remain more or less united at the base and enclose the cotyledons until they are pulled above ground by the hypocotyl (Plate I). The root establishes itself as a form of tap root and under favorable conditions elongates very rapidly, reaching a length of 3-4 inches within 48 hours. Following this, vertical growth is retarded and there is marked development of the branch roots and an extension of the hypocotyl. The branch roots first appear just below the soil surface level as early as the third and fourth days, developing later as far down as 5-6 cm. on the primary axis.

Following the rapid extension of the root, the basal region of the hypocotyl elongates and pushes the axis above ground in the form of an inverted "U" (Plate I). This results finally in pulling the unequal cotyledons and the fruit coat out of the ground, and the axis straightens into a vertical position. In many cases the plant is successful in shedding the fruit coat in this manner, while in others the remnants of the coat remain attached to the longer cotyledon for several days. The erect, pubescent, hypocotyl is oval in transverse section, increasing slightly in diameter towards the point of divergence of the cotyledons.

The gross morphology of the cotyledons has been described by Lubbock (10) as follows: "Unequal, obovate-spathulate, tapering downwards, blunt, sessile and slightly connate at the base, erect for some way above the base and then recurved, pubescent on the upper surface with a distinct midrib and two lateral nerves arising from the base, which unite with two other nerves arising about the middle of the cotyledon and run to the apex; longer cotyledon 1.4-1.6 cm. long, 5-6 mm. wide; shorter one 1-1.3 cm. long, 5.5-6 mm. wide."

Expansion of the cotyledons is rapid, after at least one is free from the fruit coat, and their lateral divergence exposes a well developed epicotyl bearing a pair of simple, opposite, leaves. The cotyledons remain foliar in appearance for 15-20 days after which they become discolored, shrivel up and finally fall off. For the first 7-10 days, the time required for the hypocotyl to reach its maximum length of 5-6 cm., the epicotyl elongates somewhat slowly. As a rule no growth is evident until after this

period and then the rate of growth is accelerated many times, and under favorable conditions the first internode reaches its normal length of 3-5 cm. by the twelfth or thirteenth day.

Subsequent development leads to the mature plant which Dewey (5) has fully described, not only for the species as a whole, but also for particular varieties. Prain (15) has investigated the floral development in considerable detail.

The first pair of leaves are simple and normally persist for a short time as compared with the life of the plant as a whole. In general the second and third pair are digitately tripartite and four- or five-partite respectively. From the third pair on up the stem and branches, the number of leaflets in the palmately compound leaf varies from 5-11, with 7 the most common number. The leaves are two ranked and opposite, the arrangement changing to alternate near the top of the stem in the older plants. The first internode is 3-5 cm. in length while the higher ones, except those close to the top of the branches and the main stem, are two to three times longer than the first. In the mature plant, the stalk attains a diameter of 3-6 cm., with a rough bark near the base. The plants are normally dioecious and, according to Dewey (5), "The staminate flowers are borne in small axillary panicles," while "The pistillate flowers are stemless and solitary in the axils of the small leaves near the ends of the branches, often crowded so as to appear like a thick spike."

The Primary Root

In connection with their studies of the secondary axis and lateral root formation, Van Tieghem and Douliot (18) concluded that the pericycle of the primary root consists of but one layer of cells. They also observed the periblem as a uniseriate layer of initials. Flahault (7), on the other hand, reports two cell layers for the periblem, but mentions no other histogen in particular. In the present investigation, all material examined showed two layers of periblem initials. With respect to the pericycle, there were no less than four layers between the protoxylem points and the endodermis, the number of layers decreasing to two in the intercotyledonary plane.

The primary root is terminated by a blunt, cone-shaped, root cap, and is diarch with two groups of primary phloem alternating with the xylem points which consist of three to five rather

thin-walled protoxylem elements. The outermost and smallest one of these elements borders on the centrad side of the pericyclic zone, and the successively larger ones are bounded laterally by parenchyma cells. The metaxylem elements, at least five in number, increase in size towards the center and in conjunction with the protoxylem elements form a wedge-shaped primary xylem region in the early stages of development. The pericycle is surrounded by a uniseriate endodermis in which the Casparian strips are but slightly developed until the time of secondary thickening. In freshly cut transverse sections, light deposits or thickenings are evident before the metaxylem has reached maturity. The cortex is composed of 5-7 concentric cell layers having conspicuous intercellular spaces and is limited centripetally by the endodermis. The outermost cortical cells form a distinct hypodermis which is similar in structure to the epidermis, except that it produces no root hairs.

The primary root develops from three well defined histogens (Plate III, Fig. D), agreeing in general with the development of the root of Linum usitatissimum as described by Janczewski (9) and Crooks (3). The root cap and epidermis are derived from a common layer of initials called a dermocalyptrogen by Erikson (6) and calyptrogen-dermatogen by Crooks (3). The cells of this layer overlying the periblem at the tip divide periclinally to form the root cap. These divisions progress laterally away from the center of the axis for only a few cell lengths when the plane of division changes and becomes anticlinal, thus transforming the histogen at this point into a true dermatogen which generates the epidermis. In each periclinal division the external daughter cell becomes a root cap member and those which are oriented into a lateral position because of the activity of the periblem and plerome at the tip may divide anticlinally. Through this anticlinal division each lateral series keeps pace with the advancing root tip until the layer becomes the outermost one of the cap and finally sloughs off. The cells in the terminal vertical rows, with the exception of possibly one or two proximal to the calyptrogen, do not undergo division, but enlarge in all three dimensions and become two to three times the size of the initials.

The anticlinal divisions in the lateral rows and the concurrent enlargement of the cells in the vertical rows result in a root cap with very regular series of cells overlying one another.

The systematic periclinal and anticlinal divisions of the calyp-trogendermatogen layer give rise to a design like an inverted stairway on the outside of the dermatogen and the epidermis, with the earliest formed step at a level common to the lower end of the region of elongation (Plate III, Fig. C).

The cortex is derived from the periblem which consists of two vertical layers which form a terminal cap over the small group of plerome cells at the root apex. The external layer of the periblem multiplies only by periclinal divisions and gives rise to a single outer cortical layer, the hypodermis, while the initials of the inner layer divide in all planes to form the remaining 4-7 layers of the cortex which are limited centripetally by the endodermis.

The stele is differentiated from the small group of plerome cells lying immediately above the periblem. Cell division near the tip occurs in all planes, while at a slightly higher level division is mainly in the transverse plane. The pericycle is the first of the tissues in the central cylinder to be differentiated and this arises from the outermost layer of the plerome. The pericyclic cells can be readily identified at an early stage in the development of the axis, since compared with those of the cortex their cell contents are considerably denser, and collated with the centripetally adjacent tissue its cells are greater in the axial dimension.

Lateral root initials arise in the pericycle early in the ontogeny of the primary root. Transverse and vertical divisions of the pericyclic cells, to form cones, take place in roots less than 48 hours old and occur down the axis to the point where the protoxylem is beginning to mature. The origin of the lateral root is approximately opposite the protoxylem point with the axis of the new root deviating 15-20 degrees from the plane of the diarch primary xylem plate (Van Tieghem and Douliot, 18).

Differentiation of the pericycle is followed immediately by simultaneous differentiation of the primary phloem and the primary xylem. The protophloem consists of elongated parenchyma cells of comparatively small diameter. The primary xylem differentiates centripetally and forms a complete diarch plate at a level less than 0.6 mm. above the root tip (Plate III, Fig. A). Coincident with this development, primary phloem ducts abutting the pericycle, on either side of the central cylinder in the inter-

cotyledonary plane, begin to mature. As many as 3-4 in each alternate phloem group are completely differentiated at a level approximately 1.5 cm. above the root tip (Plate III, Fig. B). These ducts form in a manner similar to that described by Crooks (3) for Linum usitatissimum and increase in number up to 7 or more in each primary phloem group by the time secondary growth is initiated. As secondary growth progresses, these ducts together with the other primary phloem structures are crushed against the pericycle.

Maturation of the primary xylem is initiated in the upper level of the region of elongation and progresses centripetally. Usually 3-5 thin-walled annular and spiral protoxylem elements mature first. The outermost and smallest of these elements lies against the inner layer of the pericycle, while at least two of the others border on parenchyma lying in a position where cambial activity is later initiated. The metaxylem elements mature centripetally and complete the xylem plate by the time secondary growth is begun. The elements of the metaxylem are vessels with distinctly bordered pits in which the borders are somewhat short and the torus thin. Scalariform vessels may rarely occur.

Hypocotyl, Cotyledons, and Transition

The cortex and the stele of the hypocotyl are root-like in general structure from the ground level up to a point approximately 1.5 cm. below the plane of cotyledonary divergence, except that the central region of the cylinder is parenchymatous (Plate IV, Fig. A). About 1 mm. above the ground level the centrally located metaxylem elements are replaced by thick-walled parenchyma cells. At successively higher levels the cell walls of the central parenchyma become increasingly thinner and a complete breakdown of the pith occurs slightly below the cotyledonary node in plants less than 15 days old. The elements of the metaxylem are gradually differentiated into spiral vessels, so that in the upper half of the hypocotyl vessels with bordered pits rarely occur. The pericycle may vary in number of cell layers opposite the protoxylem points, 3-5 being the more common number with usually two layers in the intercotyledonary plane. Like that of the primary root, the endodermis is not clearly defined. Its radial wall thickenings, however, become more pronounced at the time of secondary growth. The outermost of the 7 or more cortical layers forms a

well defined hypodermis. Its cell structure is similar to that of the epidermis with the exception that stomates and hairs are absent.

The cotyledons function both as photosynthetic and storage organs after coming above ground, and in the rapid growth and expansion of the same, the lamina increases in sponginess towards its apex until it is two to three times the thickness of the young epicotyledonary leaves. Stomates occur in about equal frequency in both the upper and lower epidermal layers of the cotyledon and the arrangement of the mesophyll resembles that of the foliage leaves. The cell layers in the mesophyll region, however, are more numerous, three layers of palisade comprising the adaxial half and as many as 10 layers of spongy parenchyma in the abaxial half of the lamina. These layers are clearly defined in the cotyledon before the seed germinates. The cells of both the palisade and the spongy layers are packed with reserve material in the form of large globular bodies, while the cells of the provascular strands of the cotyledon are filled with finely granular material. In the process of digestion and translocation of the reserve material, that near the apex of the cotyledon is the last to be used or may not be translocated at all, leaving a thick, spongy mass at the end.

The vascular tissue of the cotyledons is continuous with that of the hypocotyl (Plate V, Fig. D). Differentiation of the elements is initiated at the cotyledonary node and progresses outwardly into the lamina of the cotyledon and downwardly in the hypocotyl. This can be seen in seedlings less than 24 hours old where distinct collateral bundles occur and even earlier evidence may be gathered from the mature embryo where clearly defined provascular strands mark the path of ultimate differentiation. Although this is the case, in order to facilitate the account, the transition of the protoxylem from the exarch to the endarch position is here described at successive levels in an ascending order from a point in the lower hypocotyl up into the cotyledon.

The first indication of an orientation of the vascular tissue unlike that of the root occurs about 1.5 cm. below the point of divergence of the cotyledons (Plate IV, Fig. B). At this level the metaxylem begins to differentiate tangentially with reference to the protoxylem points. This arrangement results in the differentiation of the metaxylem in the form of a "V" at each

pole with the arms extended and open centripetally and the protoxylem forming the apex of this "V." Each of the alternate phloem groups is associated with an adaxial metaxylem arm and this relationship persists throughout the entire course of the transition. Concurrent with this tangential maturation of the metaxylem, a vascular strand diverges from the centrad face of each arm in the intercotyledonary plane (Plate IV, Fig. B). The two strands on either side of the cotyledonary plane converge at a slightly higher level to form the vascular bundles of the first leaves of the epicotyl (Plate IV, Fig. C). The divergence of these vascular strands and their direct association with the metaxylem of the hypocotyl may be observed in a seedling 18-24 hours old. Coincident with the maturation of the tangentially placed metaxylem and the differentiation of the epicotyledonary bundles, the pericycle becomes active, resulting in a slight increase in the diameter of the hypocotyl from this point up to the cotyledonary node. This activity is followed by the differentiation of numerous resin ducts in the phloem of the epicotyledonary bundles.

As the metaxylem is differentiated in a more and more tangential position in relation to the protoxylem it finally comes to lie in a position such that the two arms are extended in a plane at right angles to the cotyledonary plane (Plate IV, Fig. D). This may occur slightly below or at the cotyledonary node. The protoxylem at this stage lies between the two extended arms and in a line with them (Plate V, Fig. A). A complex of similar nature has been described by Thomas (17) who termed the relationship of the three primary xylem groups a "secaut" and the two primary vascular strands within a common sheath, a "double bundle." This double bundle continues outwardly and becomes the midvein of the cotyledon (Plate V, Figs. B, C).

As a rule the protoxylem is definitely endarch at the base of the cotyledon, and is isolated from the metaxylem arms by parenchyma. This relationship usually persists up to a point just above the middle of the cotyledon where the three xylem groups converge to form a single bundle.

At the base of the cotyledon, the midvein branches, giving off a lateral endarch bundle on each side, one at a level slightly above the other. Each of these lateral strands in turn branch into two principal veins. In each case the divergence directed

towards the apex of the cotyledon becomes a primary lateral vein, while the other branch descends to meet a similar divergence on the opposite cotyledon (Plate II, Fig. B). The level at which these descending veins meet is considerably lower than their point of divergence, the continuous strand thus forming a "V" in the intercotyledonary plane of the collar. Hence, if each midvein is considered as a double bundle, a total of twelve distinct collateral bundles occur in a transverse plane near the top of the cotyledonary collar (Plate V, Fig. C). In addition, two laterals, one on each side, diverge from the midvein at the point where the vascular strands of the double bundle converge. Each one of these divergences extends out to and connects with the primary lateral vein of that respective half of the lamina and then continues to the apex of the cotyledon where it anastomoses with the midvein (Plate II, Fig. B).

Summary

1. The fruit, seed, embryo, and development of the seedling of Cannabis sativa L. are described.

2. The primary root is diarch. Three clearly defined histogens occur at the growing point. The calyptragen divides periclinally at the root apex to form the root cap. Laterally this same histogen divides in anticlinal planes to give rise to the epidermis. The periblem and plerome generate the cortex and stele respectively. The cortex is limited centrifugally by a hypodermis and centripetally by an endodermis which is not clearly defined.

3. In the ontogeny of the stele, the pericycle is first differentiated. This is followed by simultaneous differentiation of the primary phloem and the primary xylem. Coincident with this the primary phloem group is marked by the maturation of 3-4 primary phloem ducts abutting the pericycle.

4. Lateral root initials are formed in the pericycle before the metaxylem matures and occur in a position approximately opposite to the protoxylem points.

5. The transition of the protoxylem from the exarch to the endarch orientation begins in the hypocotyl at a point approximately 1.5 cm. below the cotyledonary node. The complete endarch condition is attained in the lower half of the midvein of the

cotyledon.

6. The venation of the cotyledons and the cotyledonary collar is described. The two complete vascular strands of the re-oriented primary xylem constitute a double bundle and form the midvein of the cotyledonary trace.

7. Concurrent with the initiation of the transition, epicotyledonary bundles anastomose with the centrad faces of the respective metaxylem arms so that there is direct vascular connection between the first pair of epicotyledonary leaves and the hypocotyl.

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EXPLANATION OF PLATES

PLATE I

Fruit, and stages in development of the seedling. Drawn by Flowers.

PLATE II

Fig. A. Median longitudinal section of the fruit out perpendicular to the cotyledonary plane. cot, cotyledons; ec1, epicotyl; end, endodermis; fr c, fruit coat; int, integument; l, leaf; pr rt, primary root; sty e, styler end.

Fig. B. Diagram of cotyledons and cotyledonary collar showing venation. The collar has been cut open in the inter-cotyledonary plane and the cotyledons spread with the abaxial side up. coll v, collar vein; cot coll, cotyledonary collar; lv, primary lateral vein; lv', secondary lateral vein; mv, midvein.

PLATE III

Fig. A. Transverse section of primary root 0.6 mm. above root tip.

Fig. B. Transverse section of primary root 1.5 mm. above root tip.

Fig. C. Median longitudinal section of primary root.

Fig. D. Median longitudinal section of root apex showing histogens in detail.

cal, calyptrogen; co, cortex; dgn, dermatogen; en, endodermis; ep, epidermis; hd, hypodermis; mx, metaxylem; pbm, periblem; pcl, pericycle; ph, phloem; ph d, phloem duct; pl, plerome; px, protoxylem; rc root cap.

PLATE IV

Fig. A. Transverse section of hypocotyl approximately 2.5 cm. below the cotyledonary node.

Figs. B-D. Transverse sections of hypocotyl at successively higher levels showing reorientation of primary xylem, and epicotyledonary traces.

co, cortex; en, endodermis; ep, epidermis; ep hr, epidermal hair; hd, hypodermis; l, leaf trace; mx, metaxylem; pcl, pericycle; ph, phloem; pi, pith; px, protoxylem; rs d, resin duct; st, stoma.

PLATE V

Fig. A. Section of cotyledonary collar showing the three primary xylem groups in a common line and in the cotyledonary plane.

Fig. B. Section of the cotyledonary collar midway between the base of the cotyledons and the node.

Fig. C. Section of the cotyledons at their base.

Fig. D. Schematic diagram of vascular system of hypocotyl showing transition of protoxylem from exarch to endarch condition.

coll v, collar vein; co, cortex; cot coll, cotyledonary collar; ep, epidermis; ep hr, epidermal hair; hd, hypodermis; l1, l1', first pair of epicotyledonary leaves; l2, l2', second pair of leaves; l3, l3', third pair of leaves; lo ep, lower epidermis; l t, leaf trace; lv, lateral vein; mv, midvein; mx, metaxylem; pcl, pericycle; ph, phloem; pi, pith; px, protoxylem; rs d, resin duct.

PLATE I

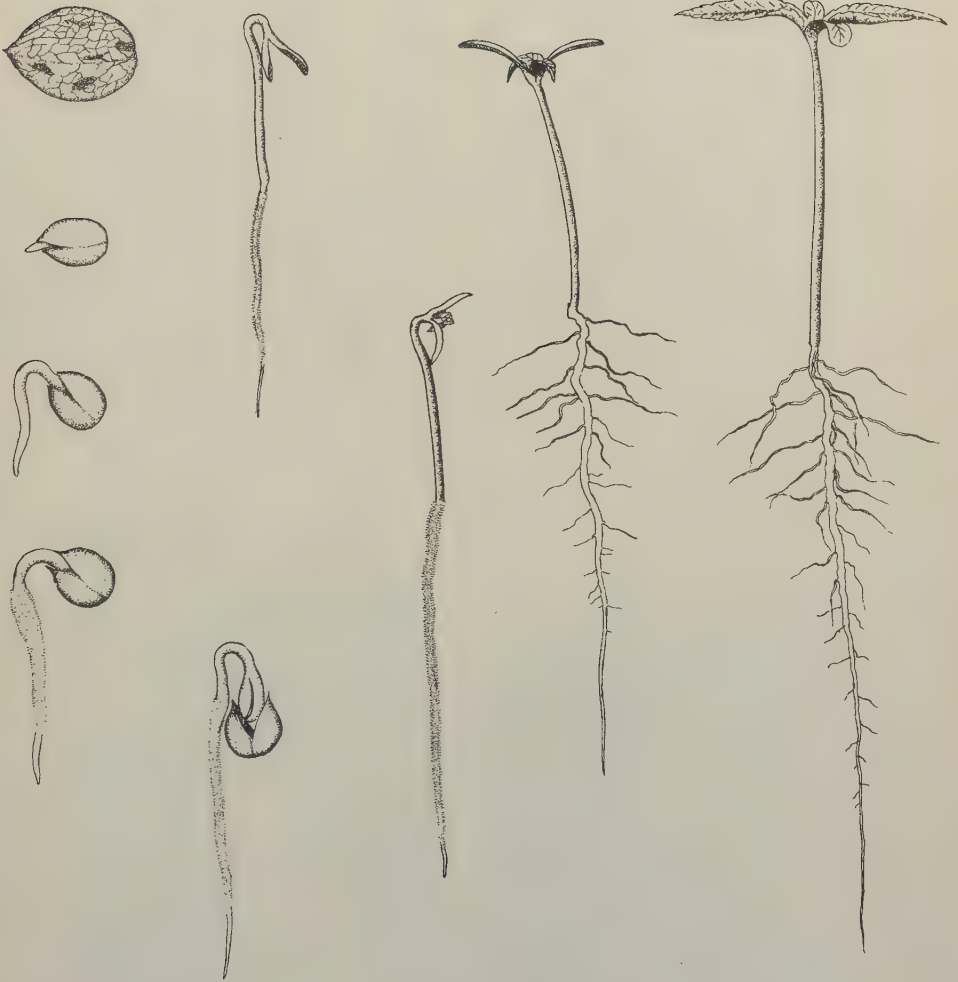
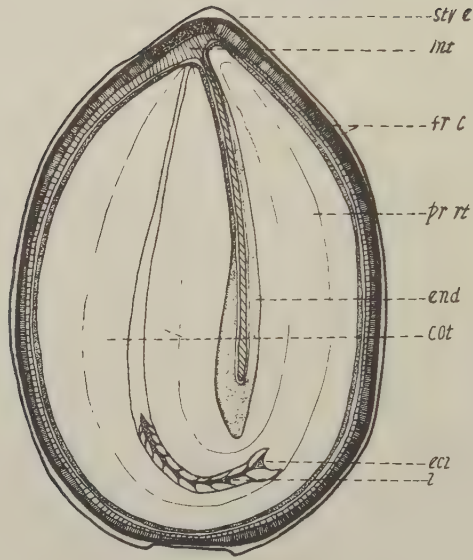
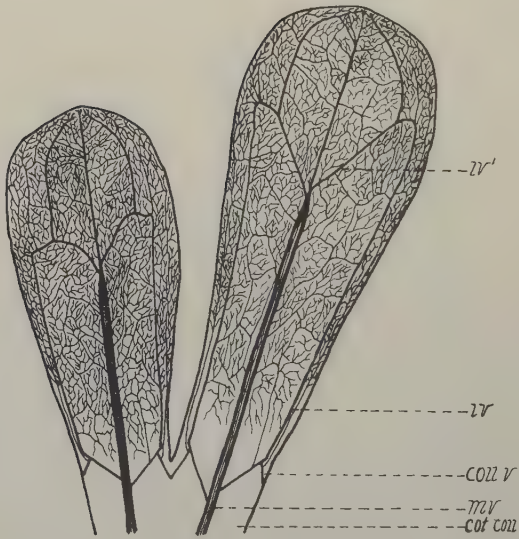


PLATE II

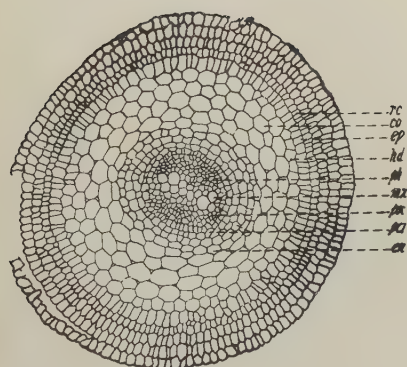


A

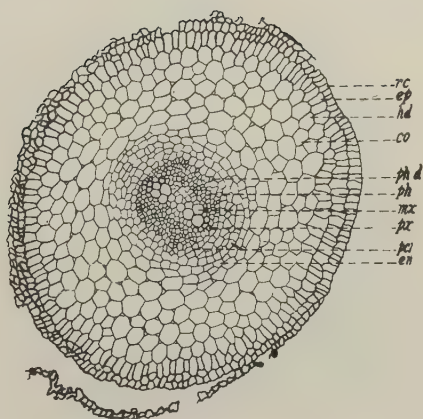


B

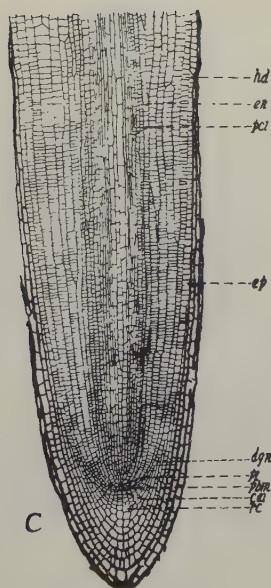
PLATE III



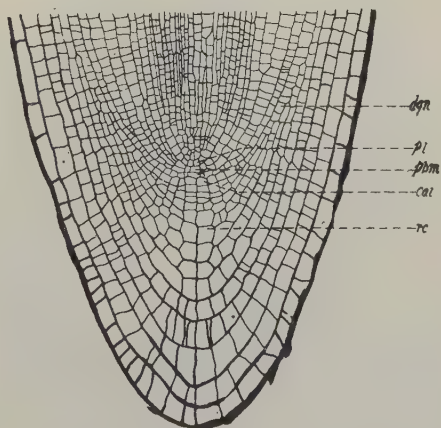
A



B

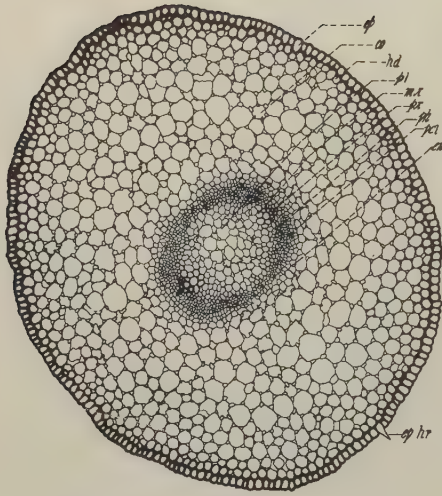


C

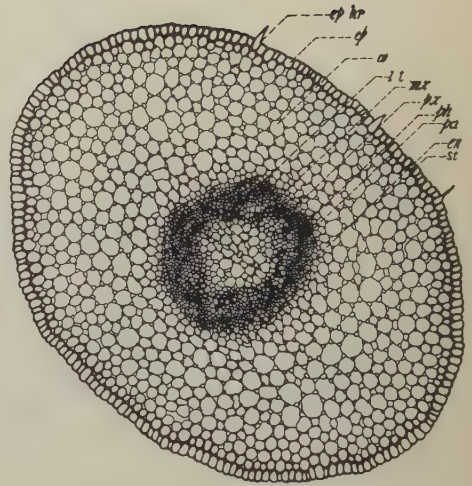


D

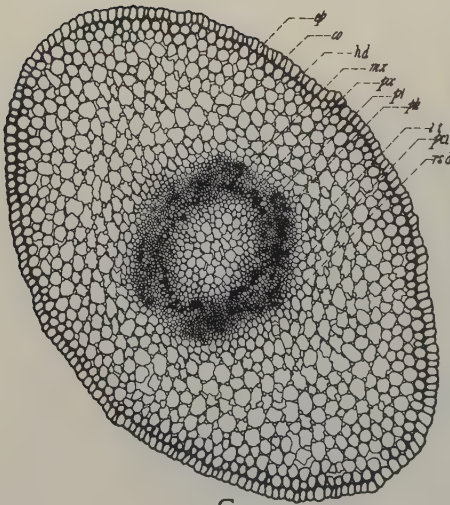
PLATE IV



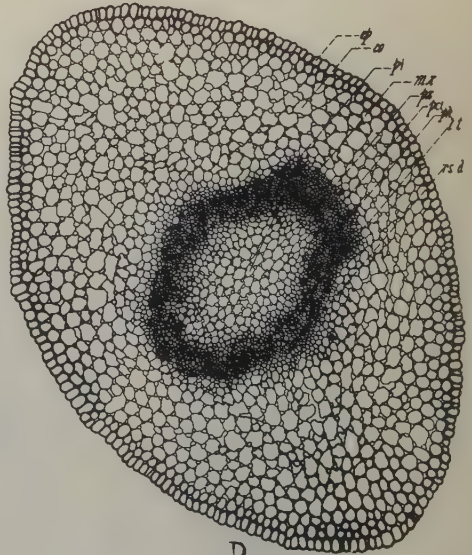
A



B

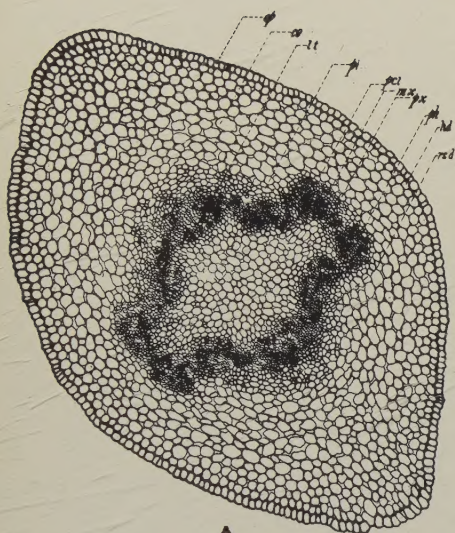


C



D

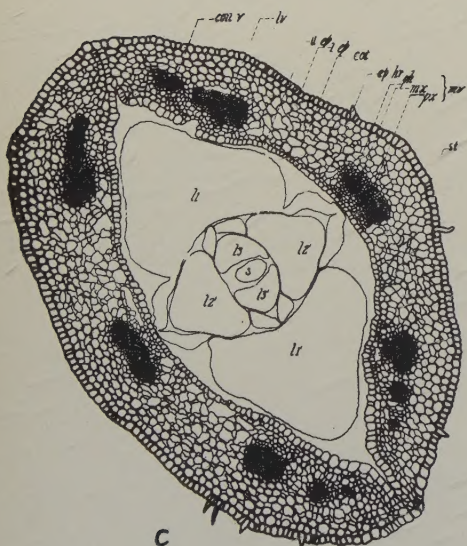
PLATE V



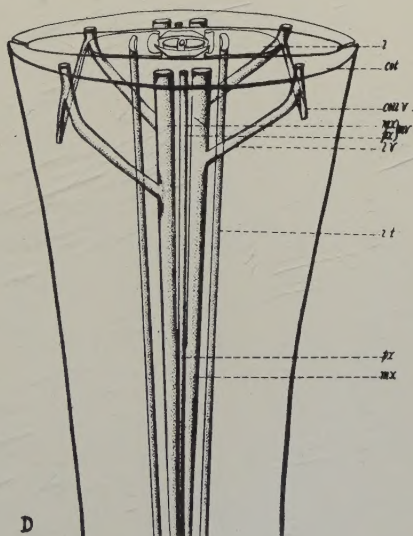
A



B



C



D

